

ANIMAL INNOVATION

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SOCIAL LEARNING: PROMOTER OR INHIBITOR OF INNOVATION?

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Introduction

During the 130-year history of the scientific study of animal behaviour, there have been two periods of relatively intense interest in the role of social learning in behavioural development. The first of these episodes occurred in the latter part of the nineteenth century at a time when instinct and imitation were considered to be the main sources of adaptive behaviour in animals. The second began some 30 years ago with the publication of Ward and Zahavi's (1973) classic paper on information centres, and continues to the present day. Below, I discuss contrasting views of the interaction of social learning and innovation characteristic of these two periods.

Social learning as a conservative force

At the end of the nineteenth century, social learning was seen as a way in which the normal behaviours of a population of animals were conserved and transmitted intact from one generation to the next. Consequently, social learning was viewed primarily as interfering with acquisition of novel patterns of behaviour.

I quote from the work of but three of the several nineteenth century behavioural scientists with an interest in the role of imitation in behavioural development. First, a paragraph from a wonderful essay by Alfred Russell Wallace (1870) entitled 'The philosophy of birds' nests.' In this brief paper, Wallace argues that constancy across generations in the structure of nests built by various avian species, like constancy across generations in the shape of human habitations, results from social learning.

'No one' Wallace asserts, 'imputes [the] stationary condition of domestic architecture among... savage tribes to instinct, but to simple imitation from one generation to another, and the absence of any sufficiently powerful stimulus to change or improvement. When once a particular mode of building has become confirmed by habit and by hereditary custom, it will be long retained, even when its utility has been lost through changed conditions, or through migration to a different region... These characteristics of the abode of savage man will be found exactly paralleled by the nests of birds' (Wallace, 1870, p. 212-5).

C. L. Morgan, writing in 1896, expressed a similar view, 'The conservative tendency of imitation, bringing the newly born members of the animal community into line with the average behaviour of the species is probably its most important office. The young bird or mammal... is born into a community where certain behaviour is constantly exhibited before its eyes. Through imitation it falls in with the traditional habits...' (Morgan, 1896, p. 183-4). Or, from an earlier monograph by the same author, 'Where the young animal is surrounded during the early plastic and imitative period of life by its own kith and kin, imitation will undoubtedly have a conservative tendency. The education of young animals by their parents has also a conservative tendency' (Morgan, 1890, p. 455).

Like Morgan, James Baldwin (1895, p. 298), the philosophically minded social psychologist, felt that the role of imitation in acquisition of novel behaviours had been over-emphasised, that 'many of the most "innate" powers of the animals are brought out, perfected and constantly kept efficient, by imitation of their own species.' Thus, imitation was to be viewed as playing an important, if sometimes underestimated, role in conservation of species-typical behaviours.

Of course others, for example Darwin's protege in matters behavioural, George Romanes (1882), saw imitation (especially of human behaviour by animals) as a source of behavioural innovations. Still, the prevailing view of imitation was that it played an essentially conservative role in behavioural development.

Social learning as a progressive force

During the past 30 years, animal behaviourists have more often been concerned with the role of social learning in diffusing novel or innovative patterns of behaviour through a population than with its possible role in maintaining existing patterns of behaviour. The list of innovative behaviours exhibited by animals that have been attributed to social learning of one kind or another is long indeed. It ranges from sweet-potato-washing by Japanese macaques on Koshima Island (Kawai, 1965) and termite fishing by chimpanzees at Gombe (Goodall, 1986) to pinecone stripping by roof rats in Israel (Terkel, 1996) and diving for molluscs among Norway rats living along the Po River in Italy (Gandolfi and Parisi, 1973).

Why such different views of social learning?

Several possible reasons for the change in perspective on the role of social learning come to mind. First, at the end of the nineteenth century, those engaged in the first scientific studies of animal behaviour were struggling to explain the observation that all the members of any given species tend to engage in similar patterns of behaviour. Today's understanding of behavioural consistency within a species rests largely on work carried out in mid-twentieth century by a large group of psychologists and biologists (e.g. Tinbergen, Lorenz, Lehrman, Kuo, etc.), and that work largely ignored the possibility that social learning might contribute to development of species-typical behaviours.

Results of Kasper-Hauser experiments convinced ethologists that behavioural transmission across generations was relatively unimportant in the development of instincts. Lehrman's (1953) reinterpretation of the results of isolation-rearing studies, focussed as it was on the importance of the interaction of individual and environment in behavioural

development, did little to undermine that conclusion. In the late 1800s, on the contrary, discussions on contributions of experience to development of species-typical behaviours focussed on social learning, particularly imitation, rather than on individual trial and error.

Second, scientists working in the late 1890s did not have access to the myriad field observations collected during the last 50 years indicating that, especially in primates, there are systematic differences in the behaviour of allopatric populations of a single species. Now that existence of such population- or locale-specific patterns of behaviour has been clearly established, these animal traditions require explanation, and social learning provides an obvious potential source of differences in the behaviour of allopatric populations of a species.

Third, scientists working in the 1890s had not been through the nature-nurture controversy of the 1960s that so clearly revealed the difficulty of determining causes of similarities in behaviour, and the comparative ease with which analyses of sources of differences in behaviour can be carried out. With the general shift in emphasis from study of sources of constancy to study of sources of variability, social learning was increasingly used to explain the latter rather than the former.

Last, we live in an era when many behavioural scientists, particularly primatologists, seek evidence of human-like performance in animals. Diffusion of technical innovations through human populations is part of the everyday experience of those of us fortunate enough to live in the twenty-first century. If, as anthropomorphic approaches to the study of behaviour require, behavioural capacities of animals in general and of primates in particular are fundamentally like those of humankind, then primates would be expected to transmit behavioural novelty.

Such increased acceptance of anthropomorphism as a heuristic (if not as an explanation) may be a necessary response to the rigid Behaviorism of the first half of the twentieth century. In any case, when anthropomorphic speculations are acceptable, the role of social learning in behavioural development is likely to be viewed differently than it was late in the nineteenth century, when naturalists were intent on rejecting the excessive anthropomorphism that characterised the work of their predecessors (Galef, 1996c).

Is there a resolution?

So, who got it right? Is social learning in animals a force for conservation of the old ways or a force for change, spreading innovative behaviours through populations? Or, are both views correct?

At least part of the answer to such questions lies in results of experiments undertaken to determine just how information is transmitted socially from one individual to another. Understanding how animals learn socially and how social learning interacts with both individual learning and unlearned predispositions of animals should provide some insight into the role of social learning in both promoting and inhibiting the spread of behavioural innovations.

Food choices of wild and laboratory rats as model systems

My students and I have used the feeding behaviour of both a common laboratory animal, the domesticated Norway rat (*Rattus norvegicus*), and of its wild progenitor, as model

systems in which to study: (1) behavioural mechanisms supporting social learning and (2) interactions of socially learned behaviours with other influences on behavioural development. Results of such studies of social feeding in Norway rats, described very briefly below (and reviewed more extensively in Galef, 1976, 1982, 1988, 1996a,b), suggest that social learning is inherently neither progressive nor conservative in its impact on behaviour. Rather, social learning acts in concert with an animal's behavioural proclivities and individual experiences, sometimes to maintain old habits in new recruits to a social group, sometimes to diffuse novel patterns of behaviour through a population.

Social learning as a conservative force in the food choices of Norway rats

Experiments with wild rats

Many years ago, my co-workers and I (Galef and Clark, 1971a) took wild Norway rats, first and second generation descendants of animals that we had trapped on garbage dumps in southern Ontario, and established them in small groups in 1×2 m enclosures. Using taste-aversion learning, we taught all the members of each of our colonies to eat only one of the two foods that we made available to each colony for 3 h each day. Our wild rats learned rapidly to avoid eating the adulterated diet placed in their cages each day and continued, for months, to avoid that diet even when later offered uncontaminated samples of it.

We then waited impatiently until young ones were born to colony members, grew to weaning age and began to eat solid food. By watching on closed-circuit television throughout daily 3-h feeding periods, we could observe and record every mouthful of food that the weaning juveniles in each enclosure ate.

We found, invariably, that the young members of each colony ate only the food that the adults of their colony were eating, and never even sampled the alternative food that adult members of their colony had learned to avoid. For weeks, the young wild rats remained faithful to the food preference we had taught to the adult members of their colony even though both adults and young were presented only with uncontaminated samples of both diets (Figures 6.1(a) and (b)).

Such avoidance of bait by young rats after adult members of their colony have been poisoned on it and learned to avoid eating it is no mere laboratory artefact. Applied ecologists trying to exterminate pest populations of wild Norway rats have reported, as we found in captive animals, that if members of an adult population learn to avoid ingesting a poison bait, their young ones will also avoid all contact with that bait for some time (Steiniger, 1950).

The reason for the socially induced conservatism in food choice seen in wild Norway rats is easy to understand. Wild rats, unlike their domesticated conspecifics, are extremely hesitant to eat any food that they have not previously eaten. For example, in the laboratory, wild Norway rats that are used to eating one food, and are then offered access only to an unfamiliar food, will often starve themselves for days before starting to eat the unfamiliar food, even if the unfamiliar food is highly nutritious and palatable (Galef, 1970). Domesticated rats placed in a similar situation will begin eating the unfamiliar food in a matter of minutes or hours.

Results of our experiments have shown that young wild rats living with older conspecifics are biased in a variety of different ways to begin eating the same food that the

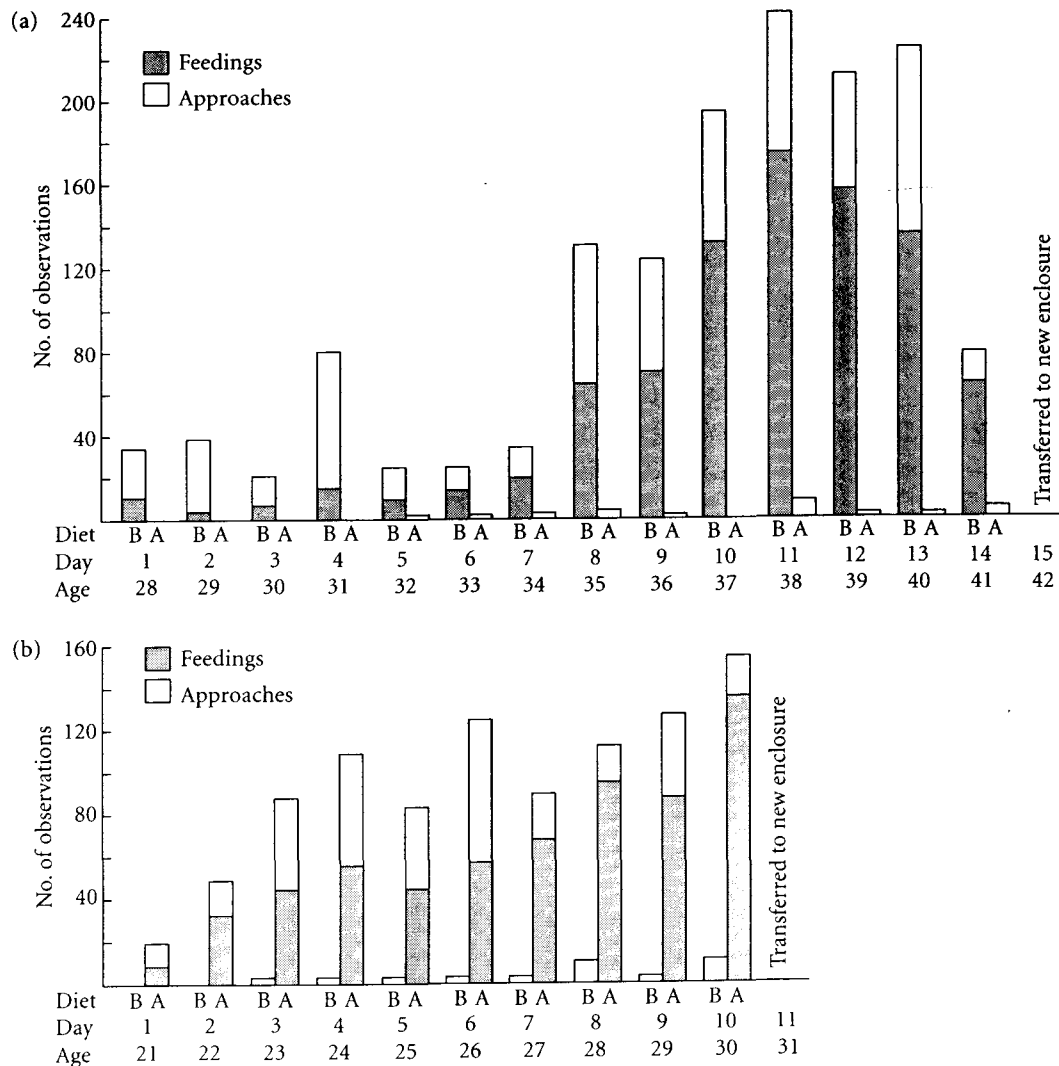


Figure 6.1 Number of observed approaches to and feedings from food bowls containing Diets A and B by weanling wild rat pups the adults of whose colonies had been trained to avoid ingesting: (a) Diet A or (b) Diet B. Reprinted from Galef and Clark (1971a) with permission. Copyright © 1971 by the American Psychological Association.

adults of their colony are eating (Galef, 1996b): (1) Young rats detect the flavour of their mother's diet in her milk and, when weaning, prefer foods having a flavour they experienced while suckling (Galef and Henderson, 1972; Galef and Sherry, 1973). (2) When seeking their first meals of solid food outside the nest, weanling rats approach adults feeding at a distance from the nest site and begin to feed close to those adults, often crawling up under an adult's belly and starting to eat under its chin (Galef and Clark, 1971a, b). (3) Young rats prefer to eat both foods and at feeding sites that have been scent-marked by adults of their species (Galef and Heiber, 1976; Galef and Beck, 1985; Laland and Plotkin, 1993). (4) Rats both young and old can detect the odour of a food on the breath of a conspecific and show enhanced preferences for foods experienced in that way (Galef and Wigmore, 1983;

Galef, 1996b). (5) Young rats show enhanced preferences for foods that they have previously stolen directly from the mouths of conspecifics (Galef *et al.* 2001), and (6) young rats follow scent trails that adults deposit when travelling from feeding sites back to their nest (Galef and Buckley, 1996).

Once weaning wild rats have been biased by interaction with adults of their colony (or with their peers) to begin eating one food rather than available alternatives, the young ones will ignore those alternatives because of their inherent reluctance to ingest unfamiliar substances. Greenberg (Chapter 8) discusses the role of neophobia, and its converse 'neophilia', in development of novel behaviours. Here we will be more concerned with the role of neophobia in maintenance of behaviours once they have been introduced into a population.

We have used comparative methods to test directly the hypothesis that the conservative nature of social influences on the food choices of young wild rats depends on an interaction between the social biasing of initial food choices and the reluctance of wild rats to ingest unfamiliar potential foods. As mentioned earlier, members of domesticated strains of Norway rat are far more willing to eat unfamiliar foods than are wild Norway rats. Consequently, although weaning domesticated rats, like weaning wild rats, might initially eat the same food that adults of their colony are eating, we predicted that domesticated rats should soon sample available foods other than the food to which adults of their colony have introduced them.

Our findings supported these predictions. Domesticated rats, like their wild forebears, initially eat the same food that adults of their colony are eating, but unlike wild rats domesticated rats soon begin first to sample and then to eat, available alternatives (Figure 6.2; Galef and Clark, 1971a). Thus, the 'neophobia' of young wild rats (their tendency to avoid

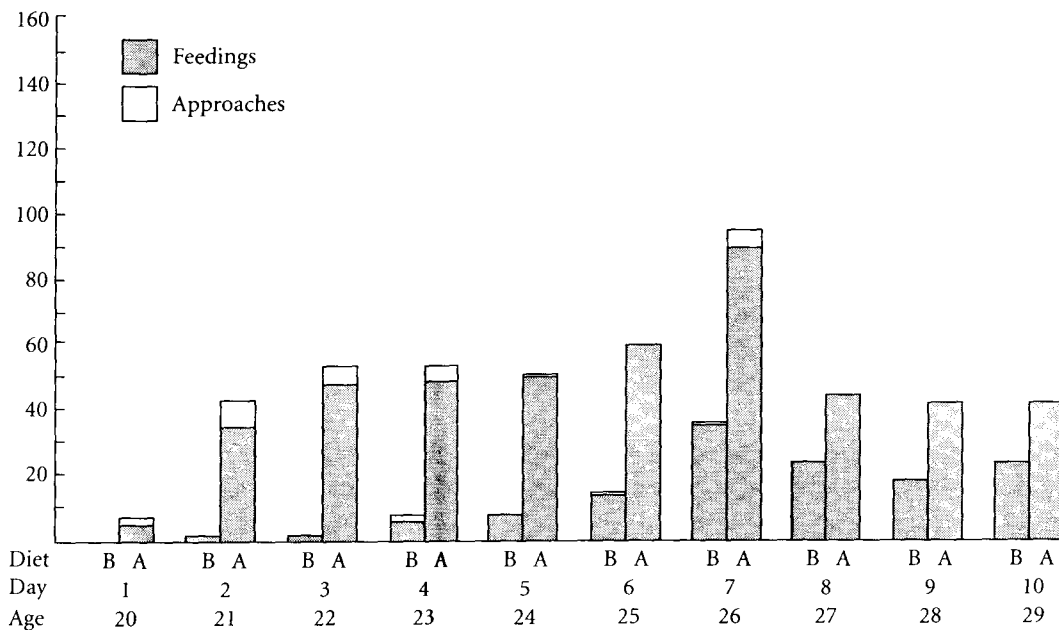


Figure 6.2 Number of observed approaches to and feedings from food bowls containing Diets A and B by weanling domestic rat pups the adults of whose colony had been trained to avoid ingesting the more palatable Diet B. Adapted from Galef and Clark (1971a) with permission. Copyright © 1971 by the American Psychological Association.

contact with unfamiliar objects or foods (Barnett, 1963)) together with social biasing of weaning rats' initial food choices, results in a highly conservative social influence on feeding behaviour.

Experiments with domesticated rats

Conservative influences of social learning are, however, not confined to neophobic wild rats and can be seen even in their domesticated, relatively neophilic descendants. As illustrated below, in domesticated rats, environmental factors can determine whether social influences conserve feeding patterns in a social group.

Evaluating consequences of ingesting various foods takes time because foods must be sampled and evaluated individually, if their relative value is to be determined accurately. Consequently, domestic rats might be expected to show stronger conservative effects of social learning on their food choices the shorter the time that they have available to determine for themselves the relative values of available foods.

We established groups of four domesticated Norway rats in 1×2 -m enclosures and again trained all members of each colony to eat one or the other of two foods placed in each enclosure, this time for 1 h/day. Once all the subjects in each colony had learned to avoid eating the adulterated food, we offered them uncontaminated samples of both foods, and they continued to avoid whichever base diet had previously contained toxin.

Once each day, we replaced one of the trained colony members with a naive conspecific. After four days of such replacement, we had a new generation, a colony of four rats none of which we had taught directly to avoid one of the foods available in the enclosure each day. After all four original colony members had been removed, we replaced each day the member of a colony that had been longest in an enclosure, and we continued this replacement process generation after generation until we exhausted our supply of naive rats.

Even after four generations of replacements, we still saw profound impact on the food choices of the last generation of the training that members of the first generation had received. Fourth-generation rats introduced into colonies whose founding members had been trained to eat cayenne-pepper flavoured diet ate far more of that diet than did fourth-generation rats introduced into colonies whose founding members had been trained to eat the alternative available diet flavoured with Japanese horseradish (Figure 6.3; Galef and Allen, 1995).

However, we observed this conservative function of social learning only when we sharply restricted the time that subjects had to sample the two foods available in their enclosures, thus denying our subjects opportunity to learn for themselves about the relative worth of the two foods. The conservative role of social learning on the food choices of successive generations of rats was far greater in rats that had access to food for 2 h/day than in rats that had access to food for 24 h/day (Figure 6.4; Galef and Whiskin, 1997). So, although domestic rats are not particularly neophobic, there are circumstances in which social learning can play a largely conservative role in behavioural development, as Wallace (1870), Morgan (1890, 1896) and Baldwin (1895) suggested was generally the case.

Social learning as a progressive force in the food preferences of Norway rats

There are also circumstances in which social learning acts progressively, to diffuse novel behaviours through a population. For example, after a naive rat (an 'observer' rat) interacts

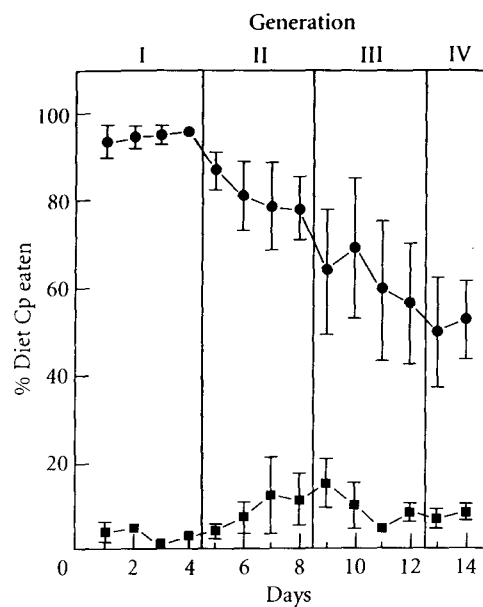


Figure 6.3 Mean amount of Diet Cp (cayenne-pepper flavoured), as a percentage of total amount eaten by domesticated rats housed in floor enclosures that contained founding colonies trained to eat either Diet Cp (circles) or Diet Jh (squares, Japanese horseradish flavoured). Day I: enclosures contained only members of the founding colony; Days 2–4: enclosures contained both original colony members and replacement subjects; Days 5–14: colonies contained only replacement subjects. Flags \pm 1 SEM. Reprinted from Galef and Allen (1995) with permission from Elsevier.

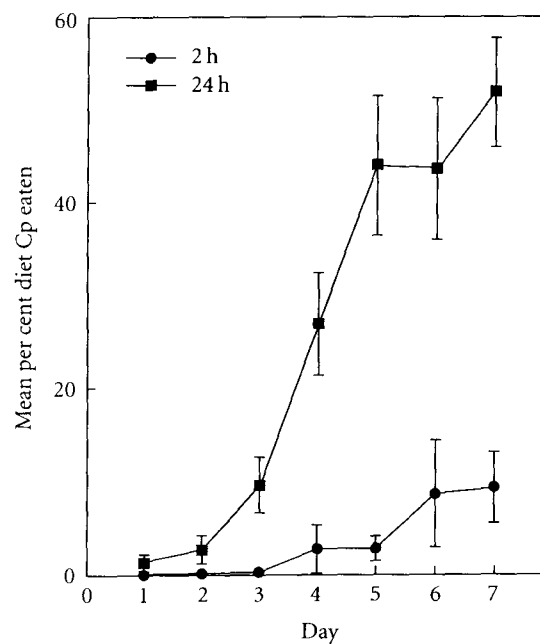


Figure 6.4 Mean amount of Diet Cp eaten, as a percentage of total intake, by founding colony members trained to eat Diet Cp and their replacements that had access to food for either 2 h (circles) or 24 h (squares) each day. Flags \pm 1 SEM. Reprinted from Galef & Whiskin (1997) with permission from Elsevier.

for a few minutes with a recently fed conspecific (a 'demonstrator' rat), the observer shows substantial enhancement of its preference for whatever food its demonstrator ate (Galef and Wigmore, 1983). In many of our experiments on such social transmission of food preference from demonstrator to observer rats, independent groups of observer rats first interacted with demonstrator rats fed either cinnamon-flavoured diet or cocoa-flavoured diet and the observers then chose between cinnamon- and cocoa-flavoured diets. Observers that had interacted with demonstrators fed cinnamon-flavoured diet preferred cinnamon-flavoured diet, whereas observers that had interacted with demonstrators fed cocoa-flavoured diet preferred that diet (Figure 6.5; Galef and Wigmore, 1983).

Of course, such a social learning process could act either conservatively to bring new recruits to a population into line with their colony's established food preferences, or progressively cause individual colony members to increase their probability of eating any unfamiliar foods being eaten by other members of their social group. Which way is this social learning process most likely to act?

To look at progressive and conservative functions of this type of social learning about foods we examined three groups of rats that were once again offered a choice between cinnamon- and cocoa-flavoured diets (Galef, 1993). Before testing for food preference, one group of subjects (whose data are depicted at the left of Figure 6.6) had no experience whatsoever of either cocoa-flavoured diet or demonstrators fed cocoa-flavoured diet. The food choices of this group of subjects provided a baseline measure of preference for the two diets. Members of a second group (whose data are presented in the middle of Figure 6.6) had eaten cocoa-flavoured diet for 3 days before interacting with the demonstrator rats that had been fed cocoa-flavoured diet. Members of a third group (whose data are depicted to the right in Figure 6.6) had never seen cocoa-flavoured diet before they interacted with a demonstrator rat fed cocoa-flavoured diet.

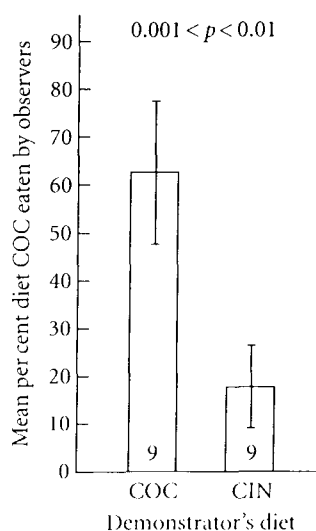


Figure 6.5 Mean amount of cocoa-flavoured diet(COC) eaten, as a percentage of total amount ingested, by observers whose demonstrators had eaten either cocoa- or cinnamon(CIN)-flavoured diet. Flags ± 1 SEM. Reprinted from Galef & Wigmore (1983) with permission from Elsevier.

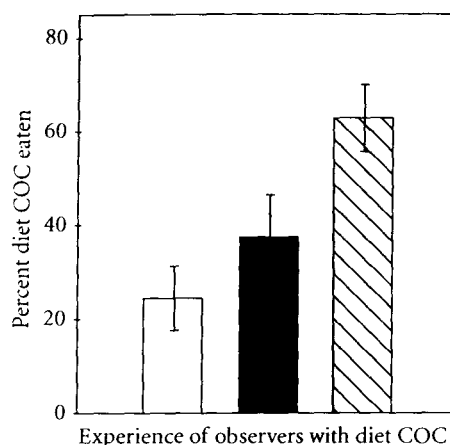


Figure 6.6 Mean amount of cocoa flavoured diet (COC), as a percentage of total amount eaten, ingested by observers when cocoa diet was totally unfamiliar (open bar), a familiar diet eaten by a demonstrator (closed bar), and an unfamiliar diet eaten by a demonstrator (hatched bar). Flags = ± 1 SEM. Reprinted from Galef (1993) with permission from Elsevier.

Comparison of the food choices of observers that were either familiar (middle bar) or unfamiliar (right bar) with cocoa-flavoured diet before they interacted with a demonstrator that had eaten cocoa-flavoured diet, shows that social-learning had a greater impact when inducing intake of an unfamiliar than of a familiar food. Such data suggest that this particular mechanism for social learning is more likely to induce population members to introduce a new food into their feeding repertoires than to continue eating a familiar food.

Commentary

The message to be extracted from the laboratory data of the sort reviewed above is that social learning can act either to conserve existing patterns of behaviour or to facilitate diffusion of novel patterns of behaviour, depending on other behavioural processes acting in an animal. Of course, social learning is only one way in which behavioural innovations can be introduced into an individual's behavioural repertoire. Individuals, especially those individuals whose established behaviours are failing to produce a desirable density of rewards, may try new ways to achieve their goal. Indeed, such individual trial-and-error must be the source of any innovative behaviours that subsequently diffuse through a population of non-human animals by social learning.

So far as we know, socially learned behaviours are neither more nor less resistant to effects of reward and punishment than are individually learned behaviours (Galef, 1995; Heyes, 1993, 1994). Consequently, frequency of expression of innovations learned socially, like that of novel behaviour patterns learned individually, will be largely determined by the relative frequency and magnitude of rewards that result from engaging in the innovative behaviour and any existing alternatives.

On such a view, when we see an innovative behaviour persevering in a population over many generations, it is reasonable to assume that it is more frequently or better rewarded than alternatives present in the behavioural repertoires of population members. For

example, Aisner and Terkel (1992) have described populations of roof rats (*Rattus rattus*) living in the pine forests of Israel that subsist on a diet consisting entirely of seeds extracted from pinecones (Zohar and Terkel, 1992). Extraction of pine seeds has been a stable tradition in these relatively short-lived animals for many decades.

Laboratory studies of development of the energetically efficient method of stripping of scales from pinecones to access pine seeds has shown that only rats reared by dams that strip pinecones efficiently learn reliably to strip pinecones in a similar way. I would suggest that, although the efficient pattern of pinecone stripping is socially learned, its maintenance in populations of forest-dwelling roof rats is a consequence of its providing greater rewards than alternative methods of attacking pinecones.

Consistent with this view is the finding that when socially learned behaviours are less efficient than available alternatives, they rapidly disappear. For example, Giraldeau and his co-workers (Giraldeau and Lefebvre, 1986, 1987; Giraldeau and Templeton, 1991) found that 'observer' pigeons tested after watching conspecifics peck open paper-covered food wells and recover seed, learned rapidly to open such wells for themselves, whereas pigeons without opportunity to learn the behaviour socially acquired it very slowly. However, when observer pigeons that had learned socially to open food wells were tested in flocks, rather than individually, some pigeons ('producers') continued to open wells, whereas others stopped exhibiting the socially learned behaviour and, instead, scrounged seed from the wells opened by producers. When Giraldeau and Lefebvre subsequently removed all producers from the flock, scroungers began, once again, to open food wells for themselves, and when producers were returned to the flock, these same birds went back to scrounging. Clearly, expression of socially learned behaviour depended on the absence of alternative routes to reward, and the longevity of the socially learned producer behaviour in individuals depended on the environmental situation, not the fact that producing was socially learned.

In sum, laboratory research with both wild and domesticated animals suggests that effects of social learning on a population can either be conservative or progressive, long lasting or ephemeral. The type and duration of social effects on behaviour of population members appears to depend on the behavioural proclivities of the social learners and on environmental contingencies, not on the fact that social processes initiated a behavioural variant.

Of course, as Laland and his co-workers have made clear in their innovative experimental work on innovation, the social environment, as well as the ecological environment, can provide rewards (e.g. Laland and Williams, 1997). If, for example, threat of predation is high and that threat is reduced substantially by remaining close to conspecifics, then ecological rewards may be foregone in the interests of social defence against predation. However, even in such cases, contingencies maintain the behaviour, not its social origins.

Implications of laboratory studies for interpretation of field observations

Controlled studies of the spread and maintenance of socially learned behaviours in convenient species should inform discussion of the origins of stable differences in behaviour observed in allopatric populations living free in their natural habitat. Failure to consider information about both the nature of social learning and the role of relative reward in

maintenance of socially acquired responses revealed by laboratory experiments, has led to some curious proposals concerning causes of differences in behaviour of allopatric populations.

For example, contemporary accounts of origins of behavioural traditions in chimpanzees require that social learning play both progressive and conservative roles. An innovative behaviour is assumed to spread through a population by social learning and then to become fixed in that population because of the presumed highly conservative nature of social learning.

In particular, Whiten *et al.* (1999), in a thought-provoking paper, described as 'cultural' two methods of tool use that chimpanzees employ when dipping for driver ants. At Gombe in Tanzania (East Africa) ant-dipping chimpanzees hold a long wand in one hand, introduce it into an underground nest of driver ants, and then quickly withdraw the wand from the nest as ants stream up the wand to attack. The feeding chimpanzee then sweeps the wand with its free hand, collecting the ants in a loose mass that it then pops into its mouth and chews rapidly to avoid being bitten (McGrew, 1992). In a second method, used by chimpanzees in the Tai forest in the Ivory Coast (West Africa), a short stick is held in one hand and used to collect a small number of ants, which are then transferred directly to the mouth by sweeping the stick through the mouth. The method of ant dipping used by chimpanzees in the Tai forest, results in far fewer ants being consumed per unit time spent ant dipping than does the technique used at Gombe (Whiten *et al.*, 1999).

If the less efficient technique used at Tai is, as Whiten *et al.* (1999) proposed, 'cultural', then, in the past, an innovator discovered the inefficient technique of ant dipping currently used by Tai chimpanzees, and that technique diffused through the Tai population by social learning. During this diffusion of behaviour, social learning had a progressive role, spreading the novel behaviour. On the culture hypothesis, either no Tai chimpanzee ever discovered the more efficient technique for ant dipping that is currently used by chimpanzees living at Gombe or learning the more efficient method of ant dipping was in some way inhibited by the socially learned, inefficient technique. In the latter case social learning would have played, and is playing, a conservative role.

It seems unlikely, for reasons indicated below, that the inefficient foraging technique continues to be used at Tai because no member of the Tai population ever discovered the more efficient technique used at Gombe. First, chimpanzees at Bossou in Guinea (West Africa), like those at Gombe, have learned to use slender wands and to gather driver ants with their hands, so, obviously, discovery of the Gombe technique occurs with some frequency. Further, and unexpectedly on the cultural explanation for the difference in ant-dipping seen at Tai and Gombe, chimpanzees at Bossou not only use both Tai and Gombe ant-dipping techniques, but also use the Tai technique (the one human observers consider relatively inefficient) more frequently than they use the Gombe technique (the one human observers consider relatively efficient). How are such data to be interpreted from the cultural perspective?

If traditions in chimpanzees are highly conservative, then a socially learned inefficient method of ant dipping might persist even if individuals at Bossou occasionally discovered the more efficient ant-dipping technique for themselves. However, as discussed previously, laboratory data suggest that socially learned behaviours are as easily modified by individual

experience of their consequences as are individually learned behaviours (Galef, 1995; Heyes, 1993, 1994). Alternatively, it is possible, though statistically unlikely, that diffusion of the more efficient method of foraging for ants is currently in progress in the Bossou population of chimps. The reason I suggest that such an explanation is unlikely is that if one examines the many behaviour patterns that Whiten *et al.* label as cultural, nearly half are habitual or common in some populations and only occasional in others. Some general explanation is required for the varying frequency of expression of population-specific behaviours in different social groups. Given the number of such cases, recency of introduction of a behaviour pattern into a population seems unlikely to be a general cause of observed variation in frequency of expression of 'cultural' behaviours.

On the other hand, and as some proponents of the 'cultural' interpretation of variability in chimpanzee behaviour have suggested: 'differences [in behaviour] could result from biotic or physical factors acting directly in transaction with the individual chimpanzee... we can never rule out unknown (to us) environmental factors' (McGrew, 1992, p. 166). Maintenance of different techniques of ant dipping in different areas might, for example, be due to differences in soil conditions, the size of ant nests, or the behaviour of nest occupants in response to intruding probes.

Of course, as the editors of the present volume suggested to me, the cultural explanation of the mixed ant-dipping behaviour seen at Bossou can be strengthened by ad hoc elaboration. For example, low-status troop members may have initiated the Gombe technique at Bossou, as low-status individuals may be more likely than high-status individuals to be innovators (Reader and Laland, 2001), and low-status individuals may be less likely than high-status individuals to serve as models for imitation (Rogers, 1962). However, a simpler explanation consistent with available data is that ant-dipping behaviours are not cultural, but instead, reflect variation in the consequences of using long and short wands in different situations.

The suggestion that ant dipping with short sticks and with long wands are efficient in different situations may be testable (See Humle and Matsuzawa (2002) for recent evidence consistent with this view). A human experimenter would first become proficient at using long wands at Gombe and short sticks at Tai. Then he or she would have to conduct an experiment using both long wands and short sticks to secure driver ants at nests exploited by chimpanzees in each location. If, in the Tai forest, short sticks caught more ants than long wands, and at Gombe, long wands were more productive of ants than short sticks, then the cultural explanation (Whiten *et al.*, 1999) for observed differences in ant dipping techniques at Gombe and Tai could be rejected.

Concluding remarks

It is, perhaps, appropriate to conclude with a quotation from Morgan (1896, p. 184). 'Often we are unable to say in the present condition of our knowledge whether the performance of certain activities is due to heredity or tradition...' To make the quote thoroughly modern, we would have to add to Morgan's proposal only 'or to individual learning about environmental contingencies.'

We know that social learning acts sometimes to spread innovation through a population and sometimes to conserve established patterns of behaviour. Possibly, social learning can

act first to introduce a novel pattern of behaviour into a population of animals and then to sustain it there without environmental support (Laland, 1996). However, demonstration under controlled conditions of this last feature of social learning is needed before it is accepted as an explanation for observed differences in the behaviour of allopatric populations living in natural habitat.

Summary

Historically, social learning has been seen as playing both conservative and progressive roles in the development of behaviour, acting both to maintain current patterns of behaviour and to spread novel behaviours through a population. Experiments investigating social influences on the food choices of both wild and domesticated laboratory rats indicate that social learning can, in fact, play either a conservative or progressive role in behavioural development, depending on environmental circumstances and the unlearned behavioural proclivities of subjects.

Consideration, from the perspective provided here, of field data describing the distribution of behavioural variants in allopatric populations of chimpanzees across Africa suggests that some purported 'cultural' differences in behavioural repertoires of chimpanzee troops may, in fact, reflect subtle differences in ecology, rather than effects of social learning. Perhaps the most pressing open question regarding social learning in animals concerns whether and under what conditions social learning can act, first, progressively to introduce a novel pattern of behaviour into a population, then conservatively to maintain the behaviour in the population in the absence of environmental support.

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